

Territorial behaviour of *Talpa romana* in two different habitats: food resources and reproductive needs as potential causes of variation

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Abstract

Differences observed in the territorial behaviour of two populations of the Roman mole, *Talpa romana*, have been explored through quantitative and qualitative analyses of food resources available in the soil. Samples of soil were collected and analysed to detect the composition and the biomass of the soil fauna. Data are related to spatial and temporal differences observed in the home ranges of the two populations. Results indicate a general inverse relationship between the availability of food and the size of territories, which is particularly evident for females. Differences in the pattern of food dispersion in the two areas are associated with the spatial distribution of female moles, which in turn relates to the territorial behaviour of males during the reproductive season.

Introduction

The Roman mole (*Talpa romana*) is a fossorial insectivore endemic to south-central Italy. Like the better known *T. europaea*, it is a solitary and territorial species, spending most of its active periods in the defence of home range boundaries and in search of food, represented by the invertebrate fauna inhabiting the soil (Loy et al. 1992, 1994 a, b). In the last four years we have carried out radio-telemetric studies in two different habitats of central Italy, an olive grove and a pasture, in order to collect data on the territorial behaviour of the species. The results revealed some differences in the spatial distribution pattern of the two populations, which mainly involved seasonal variation in the size and the relative position of home ranges (LOY et al. 1994 a, b). In an attempt to explain these differences, we focused our attention on the amount, composition and dispersion pattern of food resources available in the soil. This choice was based on the consideration that food represents the most important variable in a substantially homogeneous habitat like the subsoil (NEVO 1979), and that it is considered to be a primary force in competition among individuals (OSTFELD 1990). Moreover, according to the resource dispersion hypothesis (RDH) of MACDONALD (1983), spatial and temporal variation of resources are thought to be main factors affecting territory size and social behaviour.

Material and methods

The two radiotelemetric studies were carried out at Formello, near Rome, from February 1991 to January 1992, and at Beviglie, near Assisi, from October 1992 to May 1993. The same techniques of data recording and analysis were employed in both studies to facilitate comparisons. Results and details about techniques have already been published for the two areas (Loy et al. 1992, 1994 a, b).

Table 1. Data on home ranges (HR in m²) of animals tracked in the two habitats during the reproductive (Rep) and the non-reproductive (Non-Rep) periods, computed by the Minimum Convex Polygon method according to number of fixes (N° FIX) (data are reported from Loy et al. 1994a, b).

| PASTURE | | | | | | OLIVE GROVE | | | | | | |
|---------|------|---------|---------|--------|----------------------|-------------|------|---------|---------|--------|----------------------|------|
| PERIOD | CODE | SEX | DATE | N° FIX | HR (m ²) | PERIOD | CODE | SEX | DATE | N° FIX | HR (m ²) | |
| Non-Rep | 5F | female | Sep '91 | 100 | 813 | Non-Rep | FR1 | female | Nov '92 | 28 | 2158 | |
| | 11F | female | Sep '91 | 90 | 903 | | FE2 | female | Nov '92 | 167 | 3460 | |
| | 3F | female | Nov '91 | 190 | 3418 | | | | | mean | 2809 | |
| | 8F | female | Nov '91 | 160 | 1831 | | | | | SD | 921 | |
| | 5F | female | Dec '91 | 210 | 1844 | | | | | | | |
| | | | | | mean | | | | | | | |
| | | | | | SD | | | | | | | |
| | 9M | male | Jun '91 | 55 | 1793 | | MI1 | male | Oct '92 | 126 | 5117 | |
| | 10M | male | Jun '91 | 117 | 1537 | | MR1 | male | Nov '92 | 88 | 2304 | |
| | | | | | mean | | | | | | mean | 3711 |
| | | | | SD | | | | | | SD | 1989 | |
| Rep | 1F | female | Feb '91 | 173 | 726 | Rep | FE2 | female | Jan '93 | 154 | 1264 | |
| | 3F | female | Mar '91 | 185 | 3259 | | FR4 | female | Apr '93 | 112 | 1871 | |
| | 5F | female | Mar '91 | 99 | 877 | | FR3 | female | Apr '93 | 159 | 4621 | |
| | 8F | female | Mar '91 | 35 | 2224 | | | | | | mean | 2585 |
| | 7F | female | Apr '91 | 229 | 2152 | | | | | | SD | 1789 |
| | 5F | female | May '91 | 94 | 883 | | | | | | | |
| | 7F | female | May '91 | 334 | 1459 | | | | | | | |
| | 3F | female | Jan '92 | 149 | 2473 | | | | | | | |
| | 13F | female | Jan '92 | 105 | 2094 | | | | | | | |
| | | | | | mean | | | | | | | |
| | | | | | SD | | | | | | | |
| | 2M | male | Feb '91 | 211 | 5619 | | MI1 | male | Jan '93 | 182 | 4160 | |
| | 4M | male | Mar '91 | 261 | 4695 | | MI2 | male | Mar '93 | 128 | 2948 | |
| 6M | male | Mar '91 | 154 | 9541 | | MR1 | male | Mar '93 | 59 | 412 | | |
| 14M | male | Jan '92 | 162 | 12120 | | ME1 | male | Apr '93 | 181 | 3758 | | |
| | | | | mean | | | | | | mean | 2507 | |
| | | | | SD | | | | | | SD | 1913 | |

The first area consisted of a degraded pasture land at an altitude of 138 m where the soil was typically volcanic and characterised by stratified tufa. The other area was an olive grove in a hilly area at an altitude of about 400 m, where the soil was rich in carbonates and clay.

Fourteen moles (7 males, 7 females) were successfully radio-tracked in the pasture and 9 moles (4 males, 5 females) in the olive grove. Since some animals were recaptured and monitored more than once, the data refer to a total of 31 tracking sessions for the two areas. Details of the animals tracked and the estimated sizes of their home ranges are drawn in table 1.

The soil fauna for both areas was analysed by sampling both sites at the same time of the year, in December 1993 and April 1994, in order to account for possible changes in the invertebrate fauna during the non-reproductive and reproductive periods of moles. Ten random samples of soil were collected in each habitat, each one consisting of 64 litres of earth from a cubic pit with a side of approximately 40 cm, corresponding to the usual depth of the mole tunnels observed in the two areas. The earth was immediately sieved, and all visible invertebrates collected and stored in 70% alcohol. Invertebrates were then sorted, weighed and classified to ordinal level within a few days, in order to avoid weight loss caused by alcohol dehydration.

To verify the correspondence between the diet of the moles and the quantitative and qualitative composition of soil fauna, a sample of 18 moles, 6 males and 12 females, was kill-trapped in the olive grove in April and November 1992 and in April and November 1993, and their stomach content analysed to assess the composition of preys. All stomachs were preserved in 5% formalin, according to the method outlined by SKOCZEN (1966), and their contents weighed and then sorted and identified using a binocular microscope.

The total and relative biomasses of soil fauna found in the two areas were correlated with the average size of home ranges of males and females through multiple correlations and analyses of variance. The use of the average values was due to the lack of data on the soil fauna present inside each territory, which was in turn related to the fact that collection of soil invertebrates was performed at a different time with respect to the radio-tracking sessions. Data were analysed separately for the reproductive and the non-reproductive season. To compare the spatial distribution of soil fauna in the two areas, the Kolmogorov-Smirnov test for homogeneous distribution of the biomasses was conducted. All statistical analyses were computed using the packages SAS (version 6.0, 1985) and STATISTICA (version 4.3, 1993).

Results

The composition of the soil fauna in the two areas is shown in table 2. In terms of biomass, the fauna of both areas was dominated by Oligochaeta (percentages vary from 60% to 90% of total biomass, with the lowest values found in the olive grove). Other important groups were Mollusca, Coleoptera (larvae and adults), Dermaptera, Lepidoptera (larvae and pupae) and Hymenoptera. These other invertebrates are consistently present in the olive grove, while in the pasture they represent less than 20% of the total biomass. Thus, the soil fauna of the pasture appears less diverse with respect to the olive grove, even if almost the same number of invertebrate classes is present in both areas.

In the olive grove little variation was observed in the quantity of earthworms during different seasons, while Mollusca almost doubled in biomass during autumn-winter; the larvae of Coleoptera in the pasture land also showed a significant increase during spring (Tab. 2).

A comparison of the soil fauna composition in the olive grove and the stomach contents of moles captured in that habitat reveals that the two parameters are related (Fig. 1), with values for Pearson correlation coefficient between relative biomasses ranging from 0.96 to 0.99 ($P < 0.0001$). This evidence indicates that *Talpa romana* is an opportunistic feeder, as was already described for *T. europaea* (SKOCZEN 1966; OPPERMAN 1968; FUNMILAYO 1979) and suggests that the abundance and distribution of soil invertebrates can be used as a general indicator of food availability for moles.

Total biomass of soil invertebrates collected in the two areas in winter and spring is shown in table 2. Soil fauna in both periods was less abundant in the olive grove than in

Table 2. Relative weights and percentages of the different classes of soil invertebrates collected in the two habitats.

| TAXON | OLIVE GROVE spring | | PASTURE spring | | OLIVE GROVE winter | | PASTURE winter | |
|----------------------|-----------------------|------|-------------------|------|-----------------------|------|-------------------|------|
| | (g) | % | (g) | % | (g) | % | (g) | % |
| Mollusca | 2.4 | 11.7 | – | – | 5.1 | 22.4 | – | – |
| Oligochaeta | 13.2 | 63.4 | 26.3 | 82.0 | 13.8 | 60.0 | 48.5 | 90.0 |
| Oligochaeta, cocoons | 0.2 | 1.1 | 0.3 | 1.0 | 0.0 | 0.0 | 0.2 | 0.4 |
| Arachnida | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | – | – |
| Chilopoda | 0.2 | 0.9 | 0.2 | 0.7 | 0.2 | 0.9 | 0.7 | 1.2 |
| Diplopoda | 0.1 | 0.5 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.1 |
| Isopoda | 0.1 | 0.6 | 0.0 | 0.2 | 0.2 | 1.1 | 0.0 | 0.0 |
| Diplura | – | – | – | – | 0.0 | 0.0 | 0.1 | 0.2 |
| Protura | – | – | 0.0 | 0.0 | – | – | – | – |
| Embioptera | – | – | – | – | – | – | 0.0 | 0.0 |
| Dermaptera | 1.0 | 4.7 | 0.4 | 1.1 | 0.6 | 2.5 | 0.1 | 0.2 |
| Heteroptera | – | – | – | – | 0.1 | 0.3 | – | – |
| Lepidoptera, pupae | 0.8 | 3.8 | – | – | – | – | – | – |
| Lepidoptera, larvae | 0.6 | 3.1 | 0.4 | 1.1 | 0.4 | 2.0 | 1.6 | 3.0 |
| Diptera, pupae | – | – | 0.1 | 0.4 | – | – | – | – |
| Diptera, larvae | 0.2 | 0.7 | 0.0 | 0.1 | 0.0 | 0.0 | 0.1 | 0.1 |
| Coleoptera, adults | 0.7 | 3.3 | 0.6 | 1.8 | 0.9 | 4.1 | 1.0 | 1.9 |
| Coleoptera, pupae | – | – | 0.3 | 0.8 | – | – | – | – |
| Coleoptera, larvae | 0.8 | 3.9 | 3.0 | 9.3 | 1.5 | 6.7 | 1.6 | 2.9 |
| Hymenoptera, adults | 0.5 | 2.4 | 0.2 | 0.7 | 0.1 | 0.4 | 0.1 | 0.2 |
| Hymenoptera, pupae | – | – | 0.0 | 0.0 | – | – | – | – |
| Hymenoptera, larvae | – | – | 0.3 | 0.9 | – | – | – | – |
| Totals | 20.8 | | 32.1 | | 22.9 | | 54 | |

the pasture, an evidence confirmed by the GAMES and HOWELL (1976) test for equality of means run on the two sets of sampled biomasses in pasture and olive grove, which is significant at a level of $P < 0.05$. The total biomass in the olive grove did not change over the two periods, while in the pasture a marked seasonal variation was observed, with a greater abundance in autumn-winter.

The relation between the abundance of soil fauna and the size of territories in the two habitats was analysed by computing the correlation between the average size of home ranges of males and females during the reproductive and the non-reproductive periods, and the total biomass of soil invertebrates during the two periods. An inverse relation between territory size and the biomass of preys in the soil is shown in figure 2: a reduction in the size of territories is observed when food availability increases. The smaller territories are those of male and female moles of the pasture land during the non-reproductive season (males $x = 1\,665\text{ m}^2$, S.D. = 181; females $x = 1\,761.8\text{ m}^2$, S.D. = 1\,047.9), which is also the period of maximum abundance of soil invertebrates (54 g). The only contradictory value to the observed trend is represented by the home range size of males in the pasture during the reproductive period (coded MRP in Fig. 2). This increase of male territories during the reproductive season land has been related by Loy et al. (1994 a) to the reproductive behaviour, i. e. the active searching of sexually receptive females, rather than to trophic needs. In fact, if we exclude this contradictory value, the inverse relation between biomasses and territory sizes becomes significant ($r = -0.383$; $P < 0.05$). Results of multiple correlations between the variation of home range sizes of males and females and

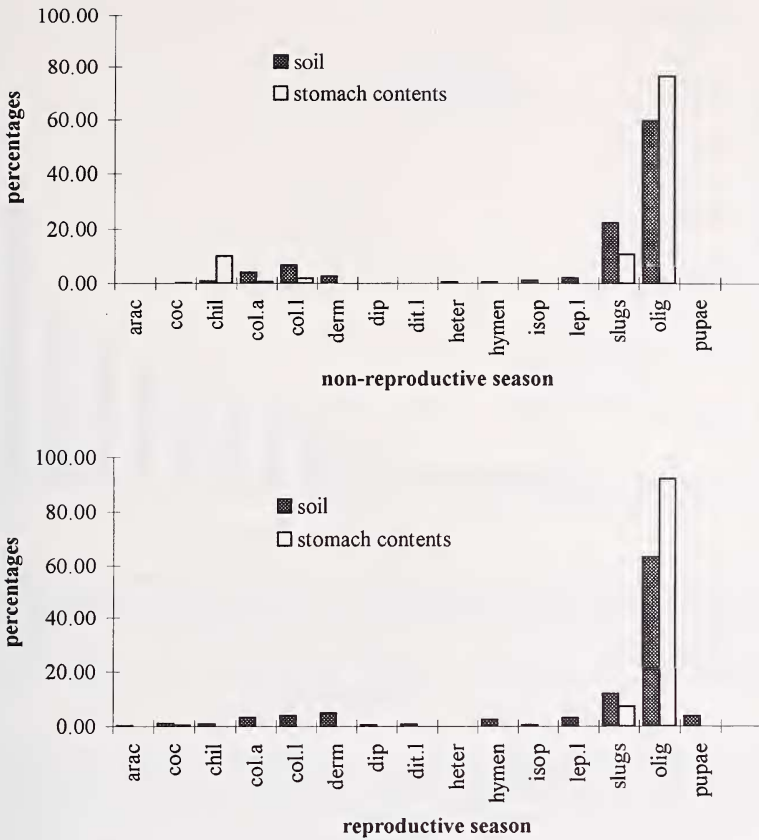


Fig. 1. Comparison between the percentages of various invertebrates found in the stomach contents of 18 moles captured in the olive grove, and in the soil fauna of the same area, analysed separately for the non-reproductive (top) and reproductive (bottom) periods (arac = Arachnida; coc = Oligochaeta cocoons; chil = Chilopoda; col.a = Coleoptera, adults; col.l = Coleoptera, larvae; derm = Dermaptera; dip = Diplopoda; dit.l = Diptera, larvae; heter = Heteroptera; hymen = Hymenoptera; isop = Isopoda; lep.l = Lepidoptera, larvae; olig = Oligochaeta).

the variation of biomasses of different classes of invertebrates, pooled over the two areas and periods, are shown in table 3.

A significant correlation is found between the size of female home ranges and the amount of earthworms, slugs, arachnida and isopods, while the size of male home ranges is related only to the minor occurrences present in the pasture solely during spring (Proctura, larvae of Coleoptera and Hymenoptera, pupae of Diptera and Hymenoptera). The only inverse significant relation is found between the size of female territories and the amount of earthworms, that always occurs in the soil of the two habitats and constitutes the greatest percentage to the total soil fauna biomass (Tab. 2).

Finally, the patterns of food distribution in the two habitats (Fig. 3) were compared through the Kolmogorov-Smirnov test for homogeneous distribution, run on the two sets of data. The test results indicate a higher d-value for the pasture than for the olive grove (pasture land: $d = 0.421$ $P < 0.01$; olive grove: $d = 0.283$ $P < 0.1$), showing that the soil fauna is more homogeneously distributed in the olive grove than in the pasture land.

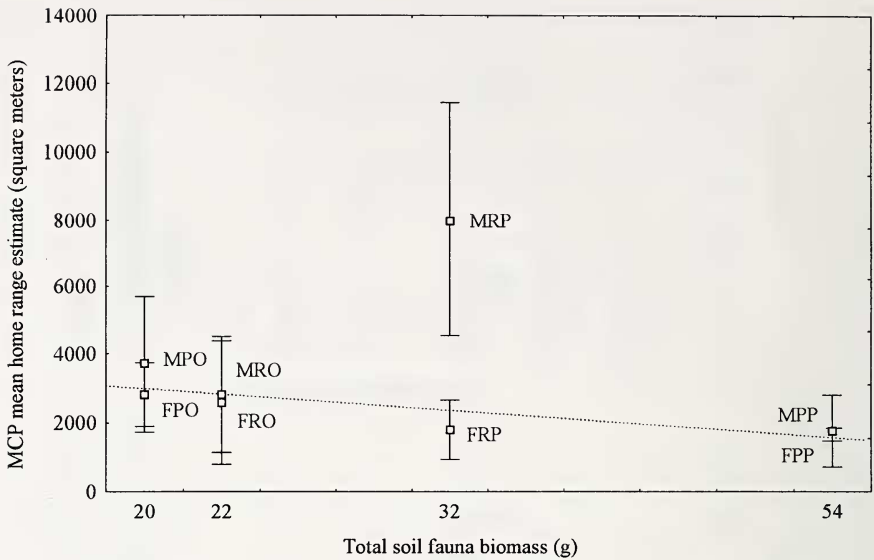


Fig. 2. Scatter plot showing the relation between total soil fauna biomass and the mean home range size of males and females in the two areas for the two periods. The first coded letter refers to the sex (M = male; F = female), the second to the period (P = pre-reproductive, R = reproductive), and the third to the habitat (O = olive grove; P = pasture). The regression line ($r = -0.383$, $P < 0.05$) has been computed excluding the contradictory value MRP, which refers to mean territory size of males in the pasture during the reproductive season (see text for details).

Table 3. Correlation between biomasses of diverse soil invertebrates and home range size of males and females, pooled over the study areas and the different seasons. Levels of significance: * = $P < 0.1$; ** = $P < 0.05$.

| | home range of males | home range of females |
|----------------------|---------------------|-----------------------|
| | r | r |
| Mollusca | -0,23 | 0,93* |
| Oligochaeta | -0,24 | -0,94* |
| Oligochaeta, cocoons | 0,39 | -0,68 |
| Arachnida | -0,12 | 0,83* |
| Chilopoda | -0,50 | -0,81 |
| Diplopoda | -0,43 | 0,03 |
| Isopoda | -0,08 | 0,94* |
| Diplura | -0,58 | -0,77 |
| Protura | 0,95** | -0,31 |
| Embiopoda | -0,58 | -0,77 |
| Dermaptera | -0,07 | 0,78 |
| Heteroptera | -0,08 | 0,71 |
| Lepidoptera, pupae | -0,30 | 0,37 |
| Lepidoptera, larvae | -0,70 | -0,69 |
| Diptera, pupae | 0,95** | -0,31 |
| Diptera, larvae | -0,42 | 0,05 |
| Coleoptera, adults | -0,75 | -0,11 |
| Coleoptera, pupae | 0,95** | -0,31 |
| Coleoptera, larvae | 0,87 | -0,41 |
| Hymenoptera, adults | -0,08 | 0,23 |
| Hymenoptera, pupae | 0,95** | -0,31 |
| Hymenoptera, larvae | 0,96** | -0,31 |

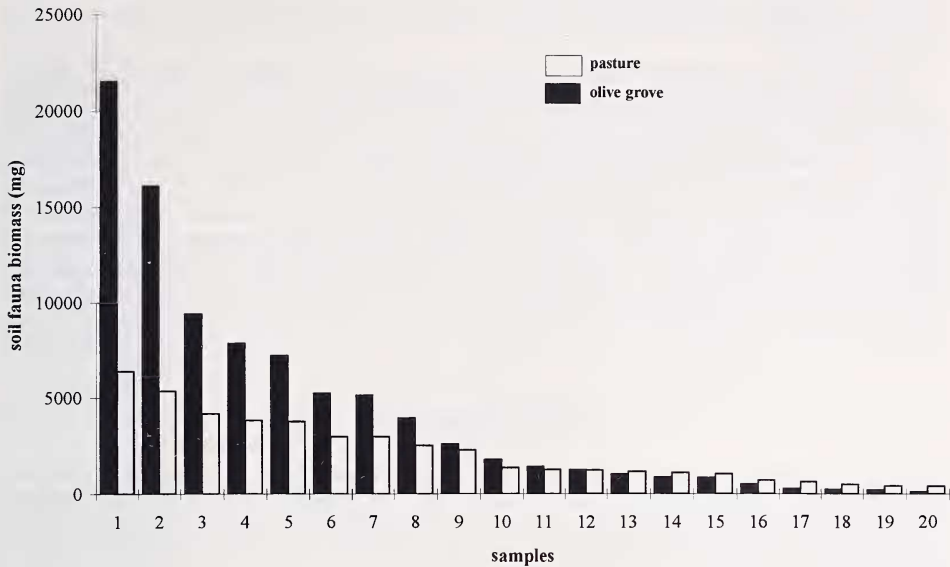


Fig. 3. Distribution of biomasses of soil fauna in each sample in the two areas.

Discussion

The relation between stomach contents and soil fauna composition confirms that *Talpa romana* is an opportunistic feeder, whose diet reflects the most abundant classes of invertebrates occurring in the soil. This feeding behaviour was already described by one of the authors in a wider sample of Roman moles (LOY 1992), and it is consistent with that described for *Talpa europaea* (SKOCZEN 1966; OPPERMAN 1968; FUNMILAYO 1979).

The territorial behaviour of male and female moles appears to be influenced differently by food and reproductive needs. According to our results, the size of female territories in both habitats is related to the availability of food, i.e. each female mole tends to defend an area, the size of which is adequate to guarantee the food supply in the long term. This consideration is also supported by other data on the territorial behaviour of the species, and particularly those regarding the use and turnover of the core areas (LOY et al. 1994 a). While this relationship between food supply and territory size is always confirmed for females, in both habitats and periods, it does not adequately explain the available data on the distribution pattern of males. The seasonal variation of the male territories observed in the pasture land suggests that this is more influenced by reproductive needs than by the availability of trophic resources. Specifically, the size of male territories appears to be influenced by the spatial distribution of females, which we suppose to be related to the kind of dispersion of food resources.

The dis-homogeneous distribution of soil fauna observed in the pasture land is likely to imply a more scattered distribution of females; as a consequence males should widely enlarge their home ranges in order to include the territories of more than one female. In this kind of habitat increased male mobility during the breeding season may become a primarily selected trait, as has been observed for other solitary and territorial species of small mammals (SCHWAGMEYER 1988; OSTFELD 1990). By contrast, a different mating behaviour should characterize the male moles in the olive grove, where a more homogeneous distribution of food resources would induce females to live in closer adjacent

territories. Therefore males do not extend their home ranges much to include those of several females.

The existence of different factors affecting the territorial behaviour of males and females is supported by the hypothesis that the mating system commonly adopted by these territorial species is a form of polygyny in which the location of sexually receptive females represents the male's main competitive hurdle for reproductive success (GORMAN and STONE 1990; LOY et al. 1994 a). Although our data are not sufficient to represent an indisputable proof for our hypothesis, they suggest that the reproductive behaviour of moles is in accordance with the general statement that among polygamous rodents and insectivores the reproductive success of males depends on access to females, while for females it depends strongly on acquisition of food (TRIVERS 1972; EMLÉN and ORING 1977; TEW and MACDONALD 1994).

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Zusammenfassung

*Revierverhalten von *Talpa romana* in zwei verschiedenen Habitaten: Nahrung und Reproduktionsbedürfnisse als potentielle Gründe der Variation*

Die Unterschiede im Revierverhalten von zwei *Talpa romana*-Populationen wurden durch qualitative und quantitative Analysen der verfügbaren Nahrungsdichte im Boden erforscht. Es wurden Bodenproben gesammelt und untersucht, um die Zusammensetzung und Biomasse der Bodenfauna zu schätzen. Die Ergebnisse wurden in Beziehung zu den beobachteten Unterschieden in der Reviergröße der zwei Populationen gestellt; es ergab sich eine umgekehrte Relation zwischen der verfügbaren Nahrungsdichte und der Reviergröße, die bei den Weibchen besonders deutlich war. Die unterschiedliche Nahrungsverteilung (homogen im ersten, inhomogen im zweiten Gebiet) wurde in Beziehung zu der unterschiedlichen Verteilung der Weibchen gebracht und diese mit dem Revierverhalten der Männchen während der Paarungszeit.

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